mended is the difficulty of obtaining high-grade material presented in an essentially geographical form. Inasmuch as this difficulty arises from the relative inattention to geography as a mature science, it is the business of geographical societies to remove the difficulty.

W. M. DAVIS.

HARVARD UNIVERSITY.

(*To be concluded.*)

---

*SOME UNSOLVED PROBLEMS OF ORGANIC ADAPTATION.**

WITH the advent of the 'Origin of Species' became current the naturalistic interpretation of organic nature, epitomized in such phrases as 'natural selection,' 'survival of the fittest,' etc. So rapid and general was the acceptance of this conception as a working hypothesis that in thirty years, or within a single generation, Wallace made bold to claim for it universal recognition in the well known and oft-quoted declaration, 'He (Darwin) did his work so well that descent with modification is now universally accepted as the order of nature in the organic world.'

As a general statement of the fact of evolution, as the phrase may be literally interpreted, it may, after fifteen additional years of intense biological activity, be as vigorously claimed and as readily conceded. If, however, it be so interpreted as to include the full content of Darwinism and the all-sufficiency of natural selection as the prime factor, with its details of endless adaptations to environment, whether physical or physiological, it need hardly be said that consent would be far less general or prompt.

Moreover, with the highly metaphysical and speculative deductions which, under the caption of 'Neo-Darwinism,' or, more plainly, 'Weismannism,' which have boldly assumed the omnipotence and all-sufficiency of natural selection to account for the least and last detail of organic differentiation or constancy, widespread doubt and open protest are too common to elicit surprise or comment.

It need hardly be pointed out at this late day, though it is more or less persistently ignored, that primitive Darwinism, while essaying to explain the origin of *species,* and emphasizing the importance of natural selection as a means in the process, did not in the least presume to account for the origin of *variation* and *adaptation,* which were recognized as fundamental and prerequisite in affording conditions without which natural selection must be hopelessly impotent. Nor, moreover, should it be overlooked that while recognizing the inseparable correlation of the factors just mentioned and their essential utility either to the individual or species in the majority of cases, Darwin was free to concede and frank in declaring the efficiency of many other factors in the intricate and complicated problems of organic evolution.

The recent impulse which has come to biologic progress by experimental methods, and the remarkable results which have been attained thereby, may without exaggeration be said to have raised anew many an earlier doubt as well as brought to light problems apparently beyond the scope of the older explanations. It may not, therefore, be an extravagant assumption to announce the entire question of organic adaptations as open for reconsideration, in the light of which no apology will be necessary for directing attention to certain phases of the subject upon the present occasion.

Among the many problems which recent investigations and conclusions have brought into better perspective as well as sharper definition, and which might profitably be discussed, the limits of a single address preclude any very wide range of

* Address of the vice-president and chairman of Section F, Zoology, St. Louis meeting, 1903.

review. I have, therefore, chosen to restrict my discussion chiefly to problems of coloration among lower invertebrates, including incidental references to correlated subjects, and the probable limitations of color as a factor in organic adaptation.

Interesting as it might be to glance at the earlier views of a subject, the nature of which from earliest times must have been a source of keen interest to mankind in general, and which must have appealed to the esthetic and rational nature, inspiring not only poetic imagery, but admiring awe and a devout fervor akin to reverence, it must suffice in the present discussion to hold attention well within the period of thought immediately concerned, which, as already indicated in the opening paragraph, was brought into prominence by the 'Origin of Species.'

As is perfectly well known, color in nature is due to one of two causes, or to a combination of both, namely: (1) What has been termed optical or structural conditions, such as diffraction, interference or unequal reflection of light, examples of which are familiar in the splendid hues of the rainbow, the iridescent sheen and metallic colors of the feathers of many birds, wings of insects, etc. (2) What are known as pigmentary colors, due to certain material substances lodged within the tissues of animals or plants which have the property of absorbing certain elements of light and of reflecting others, and thereby producing the sensation of color. While the two are physically quite distinct it is not unusual to find them associated in producing some of the most exquisite color effects of which we have knowledge. In a general way one may usually distinguish between these two sorts of color by noting that those which are purely optical in their character produce a constantly changing impression as the relative position of object or observer may happen to vary with reference to the angle and direction of light; while, upon the other hand, colors which are due to pigments show this property very slightly or not at all, and that, moreover, pigment colors are usually more or less soluble in various reagents, such as alcohol, ether, acids, alkalies, etc., and that they often fade rapidly under the influence of strong light or in its absence, or upon the death of the organism.

The presence of many and various colors in inorganic nature, the large majority of which are due to purely physical causes, such as the colors of the ocean, the sky, the clouds, the mineral or gem, while appealing to our sense of beauty elicit no special inquiry as to their significance or purpose. It suffices to know that they are constitutional or structural, inseparable from the physical conditions in which they have their place.

It is different, however, with much of the color found in the organic world. While such colors as those of the grass or leaf might seem to have hardly any different significance or to call for special explanation different from the preceding, as Wallace has pointed out, on the other hand, as he has also forcefully expressed it: "It is the wonderful individuality of the colors of animals and plants that attracts our attention—the fact that colors are localized in definite patterns, sometimes in accordance with structural characters, sometimes altogether independent of them; while often differing in most striking and fantastic manner in allied species. We are, therefore, compelled to look upon color not merely as a physical but also as a biological characteristic, which has been differentiated and specialized by natural selection, and must, therefore, find its explanation in the principle of adaptation or utility."

It is under the stimulus of this conception that the significance of color has come

to have the large place and concern in the literature of evolution which it at present occupies, as expressive of which such well-known phrases as 'protective coloration,' 'warning colors,' 'mimicry,' etc., have come to be household commonplaces among us. It is not surprising, therefore, that in a book like Wallace's 'Darwinism' out of a total of some 475 pages more than 150 should be devoted to this phase of the problem alone, while it has frequent reference in other connections.

And the same is largely true of much of the literature dealing with the subject of organic colors. In other words, color in these relations has been studied largely, if not wholly, as a factor in adaptation—fitting the animal better to meet the exigencies of life in the struggle for existence, in certain cases serving as a disguise or screen against detection, in others by glaringly advertising some noxious quality, in still others by flying a signal of alarm or warning, and in flight serving to segregate the members of a herd in whose collective aggregate a larger measure of protection might be realized.

Hence it naturally came to pass that color was looked upon largely as a physical factor in the sum total of the animal's morphology which must have some fundamental relation to the adaptation or fitness for survival of the species. It is not strange, under prevailing conditions, that small attention was directed to the more fundamental problem of the *physiological* significance of color, or the part it has to do in the processes of metabolism of the individual organism. Recent work in experimental morphology has directed attention to this phase of the problem, and one of the objects of the present discussion will be to make somewhat more evident a too long neglected aspect of animal biology.

It ought not to be overlooked in this connection that along with the development in experimental morphology to which reference has been made, those of organic chemistry, and particularly chemical physiology, have been perhaps equally important in directing attention to certain phases of our problem. Nor ought we to forget that the spectroscope has thrown its light upon the same general problem, though with perhaps less of conclusiveness than could have been desired. As a result of this growing activity there has been accumulated a body of information, a part of which stands directly related to the subject under consideration, and a part indirectly concerned with the same essential principles, and from it we may safely predict the solution of problems hitherto only predicated hypothetically, and such side-lights upon others equally important that it is not too much confidently to forecast substantial progress all along the line.

It may be well in this connection to glance briefly at some of the results at present known as in some measure justifying these somewhat optimistic assumptions, as well as pointing the line along which important and promising researches may be prosecuted.

The work of Krukenburg, MacMun, Macallum, M'Kendric, Hopkins, Urech, Eisig, Cunningham and a host of others, comprising a mass of literature of enormous proportions, will be available to those interested and may afford some faint conception of the magnitude and importance of the field to be explored, as well as an introduction to that already made available. And while as a result of this activity many and various organic pigments have been isolated and their composition in part or entirely made known, it must be recognized that the task of the chemical analysis of any such highly complex compounds as most of these are known to be is attended with extreme difficulty and no small measure of uncertainty. Still, it

has been possible fairly to distinguish several classes of such pigments, differentiated physiologically as follows:

1. Those directly serviceable in the vital processes of the organism. Under this head may be classed such pigments as hæmoglobin, chlorophyll, zoonerythrin, chlorocruorin and perhaps others less known. It need not be emphasized that by far the most important of these are the two first named. The others, found chiefly among the lower invertebrates, are believed to serve a function similar to the first.

2. Waste products. Among these the several biliary products are too well known to call for special note. Guanin is a pigment of common occurrence in the skin of certain fishes and is associated with the coloration of the species. Similarly certain coloring matters have been found in the pigments of many lepidoptera, known as lepidotic acid, a substance closely allied to uric acid and undoubtedly of the nature of a waste product.

3. Reserve products. Of these there are several series, one of which, known as lipochrome pigments, is associated with the metabolism involved in the formation of fats and oils. Perhaps of similar character are such pigments as carmine, or rather cochineal, melanin, etc. It may be somewhat doubtful whether these pigments do not rather belong to the previous class, where should probably be listed such products as hæmatoxylin, indigo, etc., all of which have been claimed as resultants of destructive metabolism in process of being eliminated from the physiologically active tissues of the body of the organism. Of similar character is probably tannic acid, a substance well known among plant products and involved in the formation of many of the brownish and rusty colors of autumn foliage, particularly of the oaks and allied trees, as are the lipochromes in the formation of the reds and yellows which form so conspicuous a feature among autumn colors.

While the association of these and other pigmentary matters has long been known in connection with both animal and plant growth, and while the conception of their more or less intimate relation to the active metabolism of the various tissues is not new, comparatively little has been done toward directly investigating and elucidating the exact nature and extent of the process. This seems to be especially the case in relation to the part played by these products in the formation of those features of coloration among organisms with which we are now concerned.

The most strenuous advocates of the primary importance of natural selection as the chief or only factor in adaptation are free to admit that among the simplest forms particularly, color has originated in some more or less obscure way through growth or some of the vital activities of the organism, Darwin, for example, merely suggesting that 'Their brightest tints result from the chemical nature or minute structure of their tissues,' and Wallace in the even less explicit statement that 'color is a normal product of organization,' whatever that may imply.

So far as I am aware Eisig was among the earliest to claim that among certain annelids the colors were primarily expressions of the katabolic processes of the tissues, and were excretory in character. He was able largely to demonstrate this with species of Capitellidæ by experimental methods. By feeding the animals with carmine he was able to follow its course through the alimentary tract, its progress through the tissues, and final deposition in the hypodermal tissues beneath the cuticle, where in the process of moulting it was finally eliminated. He also found that in a species of *Eunice,* which fed upon sponges, the pigment granules of the food

passed unchanged through the intestine and into the body tissues much as had been the case in the experiments with the preceding.

Graff later reached very similar conclusions concerning coloration in the leeches, but was able to go a step farther than Eisig had done and to show in great detail the exact process through which it was brought about. He found in the endothelium certain migratory cells which wander about in the cœlom or penetrate through the tissues, and that among their functions one of the most important seems to be the absorption of foreign bodies and their conveyance into the mouths of the nephridia or through the tissues to the hypodermis and their lodgment in that tissue. He was even able to show that the special markings or color patterns which are so characteristic of the animals may be explained by the disposition of the muscle bands, and their relation to the lines of pigmentary deposition by the wandering cells, which Graff has designated 'excretophores.' He was also able to confirm the results of Eisig as to the experimental demonstration of feeding with various pigmentary matters, and subsequently tracing them from point to point in the process of elimination. Furthermore, he showed that the amount and density of pigmentation was closely related to the intensity of metabolism, being greatest in those specimens which were most voracious feeders.

Observations of a similar character have been made upon certain of the protozoa, particularly upon *Stentor*. Schuberg in 1890 found that the blue-green pigment so characteristic of this organism was constantly being excreted bodily in the form of definite granules.

In 1893 Johnson, in an extended study of the morphology of these protozoa, confirmed the preceding observations, and showed that the pigment was excreted along with other excrementitious matter. He found also that the principal region of excretory activity was at the base of the animal, where was formed after a short time a definite mass of debris near the foot.

Perhaps one of the most important contributions along this line is that of Harmer on the character of the 'brown body' of the polyzoa. By a series of critical observations upon the life-history of these interesting organisms and painstaking experiments in feeding with carmine and other pigments, he was able to prove beyond reasonable doubt that the so-called 'brown body' of the polyzoa is a direct product of the destructive metabolism within the body and its excretion in a mass at this particular region. He found that the leucocytes of the funicular organ as well as certain cells of the organ itself engulfed pigmentary wastes, and with the periodic decline of the polypides these cells became crowded into a close mass, thereby constituting the 'brown body.' The new polypide arising by a sort of regenerative process was found to be always devoid of any coloration, no pigment appearing for some time following the activity of the new polypide, but that it is formed in regularly increasing amounts with the age and degree of metabolism of the organisms.

Correlated with these views concerning the origin of certain colors and their disposition in the organism is that of the relation of coloration to the food. It has long been known that in many cases there is a more or less intimate relation of color to the food consumed by certain animals. Instances of this are too numerous for detailed consideration here. Let it suffice that Darwin, Semper, Eimer, Koch, Beddard, Poulton, Gunther and many others have, by extended observations and by detailed experimentation, apparently established the general fact. Beddard quotes the following observation made by G.

Brown-Goode as to such an explanation of protective coloration in fishes. "On certain ledges along the coast of New England are rocks covered by dense growths of scarlet and crimson seaweeds. The codfish, the cunner, the sea raven, the rock eel, and the wrymouth, which inhabit these brilliant groves, are all colored to match their surroundings; the cod, which has naturally the lighter color, being most brilliant in its scarlet hues, while others whose skins have a large and original supply of black have deeper tints or dark red and brown." He then quotes farther the suggestions of Goode that these colors are due to pigment derived either directly or indirectly from the red algæ; those which are carnivorous feeding upon the crustacea and other marine organisms whose stomachs are full of the algæ and their pigments which pass unchanged into the tissues of the fishes.

He also quotes a similar conclusion of Gunther as to the origin of the red pigment of the salmon being derived from the red pigment of the crustacea upon which it feeds. While admitting that in the cases just cited there has been no attempt at demonstration of the proposed explanation, it yet would seem highly probable. "It is too remarkable a coincidence that the fish normally with but little pigment should when among these weeds be *bright red,* and that the fish normally possessing black pigment should be *dark red,* to permit of a settlement of the question offhand by the easy help of natural selection —without at least some further inquiry."

With the foregoing considerations concerning the general origin and development of pigments and their relations to the colors of organisms, we may next proceed to pass rapidly in review such groups of animals as we may choose to consider, and may institute a brief inquiry as to the significance of their types of coloration as factors of adaptation.

With the avowed purpose of restricting my observations and discussion as far as practicable to the lower groups of invertebrates as already announced, it will suffice to say further that in justification of such a course I am constrained to consider the lower animals, particularly cœlenterates, as more favorable subjects from which to obtain fundamental conclusions than are the more highly specialized insects or birds which have had so large a measure of attention in earlier investigations along these lines.

Furthermore, it seems highly probable that future investigations will involve more of direct experimentation than has hitherto been the case, and if so, these lower series will naturally afford some of the best material available for such inquiries, not only because of the more ready and rapid responses obtained, but from the relative simplicity of their organization and the consequent simplicity of results likely to be obtained in each case.

If further warrant were demanded for a comparatively limited survey, or special emphasis upon a limited group of animals, I should find it in a measure in the personal interest and familiarity which has come from special researches connected therewith.

Beginning with the hydrozoa it may be noted in the outset that though including the simplest of the Cœlenterates we shall find a remarkable variety and range of coloration. Among the hydroids, as is well known, coloration is neither very remarkable as to brilliance nor distribution. Many, if not most, are almost without color distinction, except in the dull brownish or amber colors found in such as *Obelia, Halecium,* and other campanularians. This may be due in part to the fact that the colonies are so generally encased within a chitinous perisarc which, while somewhat colored as already indicated, is

seldom if ever of any considerable brilliance or diversity. Among the tubularians, in many of which the development of a perisarc is slight, and always lacking over the hydranth itself, there is often found considerable coloration, as in *Eudendrium, Pennaria, Corymorpha* and others. And in these color is usually found associated more particularly with the development of the sexual products, or during the season of reproductive activity, which is a matter of considerable significance, to be taken up in a later connection.

As is well known, the predominance of alternation of generations in these animals brings into prominence the sexual phase, which in most species is an independent organism—the medusa. And it is in connection with the medusæ that we find the most marked development of color. There does not, however, appear to be any well-defined distribution of colors into patterns. Among the Hydromedusæ the distribution of pigment, which is almost the only conspicuous kind of color present, is chiefly in association with the gonads, the tissues of the stomach and the regions of the chymiferous canals, though in some cases also extending to the tentacles and in the regions of the sensory organs. It should not be overlooked, however, that in many of these medusæ the color tints are among the most beautiful and delicate known, though lacking the intensity more common among the Scyphomedusæ and corals.

Turning attention to the Scyphomedusæ we find as just suggested a more copious development of color, and also what is more significant, in many cases its distribution into something like definite patterns, as is more or less evident in such genera as *Cyanea, Pelagia* and *Rhizostoma*. It is, however, no less evident that among these we have, as in the former, the deposition of pigment along the lines of most active metabolism, such as the gastrovascular and reproductive organs, in most abundance and usually of greatest brilliance.

It is, however, when we come to the Anthozoa, which includes the corals, actinians, sea-fans, etc., that we find the climax of coloration, both as regards brilliance and intensity. To look into the crystalline depths of the waters about a coral reef where these varied forms thrive in great garden-like areas is to gaze upon a scene, the fairy-like features of which it would be difficult to exaggerate. Here are actinians, corals, sea-fans, sea-feathers, etc., which abound in the richest profusion and endless variety, seeming to vie with each other in the effort to produce the most exquisite displays of every tint of the spectrum.

In the distribution of color there is not apparently any advance as to differentiation over that found in the Scyphomedusæ, if indeed as much, though among the actinians certain stripings and mottlings occur over the exterior of the body. It is worthy of note that in those forms in which the tendency toward definite coloration is more evident there appears to be in many cases considerable variation of coloration. This is particularly noticeable in such forms as *Metridium* and *Cyanea*.

Face to face with this rich profusion and beauty of color what is its significance? How has it originated and what does it mean? Is it simply the expression of some original constitution peculiar to the entire class, and if so why does it differ in so marked a degree among the different subclasses? We may safely dismiss such an alternative as altogether unnecessary and without value as an explanation. May it be considered as an adaptation to protection, the result of natural selection? Certainly in no direct sense, for without exception, so far as I am aware, the more

brightly colored forms are thereby rendered correspondingly more conspicuous and, therefore, more liable to attack from enemies. May it come within the category of 'warning' coloration, due to the offensive cnidarian armor borne by most of the members of this phylum? So not a few who have essayed an account of the matter would have us believe. It seems to me, however, open to serious doubt, aside from the fact that it lacks evidence. On the other hand, among hydroids I have found that those having brighter colors are most liable to be eaten by fishes in the habit of feeding upon such a diet. Furthermore, various worms, snails, etc., which are known to feed upon them would be more likely to be attracted by colors than to be repelled. It is also matter of common observation that such animals are much more abundant among colonies of highly colored hydroids like *Eudendrium, Pennaria* and *Tubularia* than among species of *Obelia* or others of little color distinction. Many fishes with finely adapted dental apparatus are constant feeders upon corals, tranquilly browsing among the animated foliage of this luxuriant forest.

Finally, may it come within the category of 'sexual selection'? So far as I am aware, no one has ventured to assign to it any such a significance. Where sex characters are so little differentiated as among at least a portion of the phylum such an explanation would be as far-fetched as it would be unnecessary. While upon the part of some of the older naturalists there was a disposition to regard the massing of members of the Scyphomedusæ at certain times as having a sexual meaning, it may be doubted whether it has any considerable support in facts.

Concerning coloration among the anthozoa, Duerden, whose work on the group is so extended and so favorably known, has summarized the following account:

"The prevalence of the yellow and brown color is easily understood when an examination is made of the polypal tissues. For in all instances in which it occurs, the entoderm is found to be crowded with the so-called 'yellow cells' or Zooxanthellæ, which are unicellular, symbiotic algæ, the chromatophores of which are yellow or yellowish-green. That these are the main cause of the external coloration may be easily proved from colonies of *Madrepora*. In this genus the polyps toward the apex of branches are nearly colorless, and on a microscopic examination of the entodermal layer Zooxanthellæ are found to be absent while they are present in abundance in older pigmented regions."

These symbiotic algæ are not, however, the only source of color among the corals. Duerden finds ectodermal pigment granules, aggregated in somewhat irregular, isolated patches in some cases, in others somewhat regularly distributed.

He also found that a third source of coloration among corals was the presence of what he has termed 'boring algæ.' These were both red and green, and penetrate into the skeletal mass and color it a distinct red or green, as one or the other may be present.

In his work on the Actiniaria of Jamaica, this author has found in many cases the presence of unicellular green algæ growing upon the surface and giving to the polyp a distinctively green color. He found also superficial granular pigments in certain species which could be removed by any erosion of the ectoderm. I have found the same in several species of New England actinians, and in some cases the pigmentation was irregularly distributed, sometimes in blotches, sometimes in longitudinal stripes, more often the latter. So extremely variable is the coloration in many of these organisms that it is impossible to utilize it as a factor in differentiating spe-

cies. Duerden has called attention to this feature among both corals and actinians, and believes it to be due to the presence or absence of greater or less intensity of light, and believes it to be an expression of the fact that the Zooxanthellæ are not able to thrive except under proper light, and that, moreover, where light is too intense, as in shallower waters, certain dark pigment found in such specimens is thought to be due to its utility as a screen. While there may be a measure of credibility as to phases of this view, it does not seem to me as of general adequacy. The variability of species to which I have just referred and to the very common genus *Metridium* is certainly not due in any appreciable degree to the factor of light, since it occurs indiscriminately among specimens taken in identical situations as well as under those of differing conditions.

In this connection may be mentioned the same phenomenon among medusæ. The variation of coloration in *Cyanea* has long been known and is so marked that the elder Agassiz distinguished two additional species chiefly on this character, both of which have long since been discarded. It is quite well known to observers that these animals when placed in aquaria usually show within a very short time a more or less marked diminution in colors. *Dactylometra,* while living fairly well for many days in the aquarium, loses within this time so much of its usually bright coloration as not to seem like the same creature. The same is true of many other animals than medusæ. On the other hand, it is equally well known that many other animals may be placed under these more or less artificial environments with little apparent loss in this or other respect. That it is not due to light alone is evident in the fact that similar changes occur in medusæ which have been kept in open pools or enclosures about docks or elsewhere.

It seems to me rather that the true explanation is to be found in the changed conditions of nutrition and the consequent change in the metabolism of the animal. Hydroids placed under these conditions show the same tendency.

Those which take kindly to the change show no appreciable decline as to color or other vital process. The same is true of medusæ. *Gonionemus* may be kept for weeks in the aquarium, and if properly fed will show no decline in color, while if the conditions become bad an immediate change is noticeable in this as well as other features.

The same may be said concerning the actinians. While many seem to suffer noticeably when placed in aquaria others show no apparent difference. *Cerianthus membranaceus,* one of the finest of the actinians to be seen in the Naples aquarium, and one of the most variable, shows no apparent decline in any vital function. Specimens have been kept in flourishing condition in the aquarium for several years and show no sign of decline, the coloration continuing as brilliant as in the open sea. The same is true of many other organisms found in finest condition in this celebrated aquarium. Among the annelids *Protula* soon shows decline in color vigor, and the same is true, though to a less degree, in the case of *Spirographis* and *Serpula.*

While it may not be without probability that some measure of this color change may be due in certain cases to the changed conditions of light, it still remains true, I believe, that light alone is but a single factor, and that often a minor one involved in the changes observed, and that changed conditions of nutrition and metabolism are by far the more important.

The main factor of our problem, however, is still unsolved. What answer shall we make to ourselves concerning the sig-

nificance of the multiform colors more or less general among members of the cœlentera? It seems to me more or less evident that natural selection can have at best but a limited place in its explanation. I see no place for it along the lines of protection, either direct or indirect.

Of even less significance can any modification of it under the guise of sexual selection be claimed; for even aside from the large majority of cases where there is slight if any sex differentiation, no sensory organization, which Darwin recognized as essential to the exercise of this factor, is present through which it might become operative in even the smallest degree.

Two, and only two, other methods of explanation have seemed to me to afford a reasonable account. First, that it is due primarily to the normal course of metabolism, during which color appears as one of its many expressions. Darwin himself was not indifferent to this possibility, and expressly states in connection with the same problem that color might very naturally arise under such conditions. "Bearing in mind," he suggests, "how many substances closely analogous to organic compounds have been recently formed by chemists, and which exhibit the most splendid colors, it would have been a strange fact if substances similarly colored had not often originated, independently of any useful end thus gained, in the complex laboratory of the living organism." It has also been pointed out in an earlier portion of this paper that Wallace had to appeal to a similar source in his search for the primary factors of animal coloration.

Geddes and Thomson in discussing the problems of sex likewise make a similar claim. They declare, "pigments of richness and variety in related series, point to preeminent activity of chemical processes in the animals which possess them. Technically expressed, abundant pigments are expressions of intense metabolism." They further find in the phenomena of bright colors among the males of most of the higher animals simply the expression of the correspondingly greater activities of the process of metabolism.

I believe that in this source we have a real account of a considerable body of color phenomena among the lower invertebrates, and particularly of that series under present consideration.

The second factor to which I would appeal is so nearly related to the former as to be involved more or less intimately therewith. It is to the effect that certain pigments are products of waste in process of elimination. This has already been referred to in a former connection and need not be separately emphasized apart from the concrete cases to which it may be applied.

Strongly significant of the importance of this process among the Hydrozoa is the fact already pointed out that pigments are found deposited along the lines of principal metabolism, namely, the gastrovascular regions, the gonads, and to a less extent the immediate regions of sensory bodies, when these may be present. While this alone as a mere statement of fact does not prove the point at issue, when taken in connection with other facts of a similar nature, it amounts to a high degree of probability.

What evidence have we that in the case of hydroids, medusæ, etc., colors are associated with excretory processes? While the facts are not numerous, they are, I believe, rather convincing. In work upon regeneration in hydroids, Driesch and Loeb called attention to certain pigmentary matters found in *Tubularia* and

claimed for it an important function in the regenerative process. Morgan, and later Stevens, working upon the same hydroid, became convinced that the claims of the former investigators as to the importance of this pigment were not well founded. They found that not only was the pigment of no special importance, but that it was *really* a waste product, and that during the process of regeneration was actually excreted and finally ejected bodily from the hydranth. I have personally been able to confirm these results on the same and related hydroids, and have also shown that in regenerating medusæ there is formed *de novo* in each regenerating organ, such as manubrium, radial canals, etc., the characteristic pigment of the normal organ. This was particularly noticeable in the case of radial canals. Following their regeneration and promptly upon their functional activity the deposition of pigment made its appearance, and within a comparatively short time had acquired the normal intensity. This was also true of other organs, tentacles and tentacular bulbs, as well as manubrium and canals.

Substantially the same results have been obtained, though here first announced, in experiments upon one of the Scyphomedusæ. In very young specimens where the tissues are delicate it is possible to note the intense activity in regenerating organs, such as the sensory body. The first part of this organ to make its appearance is the sensory papilla, which is soon followed by the otoliths, and later by the special pigmentation of the entire organ.

From the foregoing considerations three things seem to me to be more or less evident:

1. That in all regenerative processes a very marked degree of metabolism is involved, whether in the mere metamorphosis of old tissues into new, or in the direct regeneration of new tissues by growth processes, both of which seem to occur.

2. That in regenerative processes there is often associated the development of pigmentary substances which seem to have no direct function in relation thereto.

3. That in many cases there follows a more or less active excretion and elimination of portions of the pigment in question.

Concerning color phenomena among the several classes of worms we are in much the same uncertain state of mind as in the former. For while in some of the annelids there may be found fairly well developed visual organs it may be seriously questioned whether they are of any such degree of perfection as would enable their possessors to distinguish small color distinctions. And if this be the case there would at once be eliminated any possibility of conscious adaptation in seeking a suitable environment, or such as would be involved in so-called sexual selection.

Furthermore, it is very well known that among this group some which exhibit among the richest of these color phenomena have their habitat in seclusion, buried in sand or mud, or hidden beneath stones, or with tubes built up from their own secretions, or otherwise so environed as to render practically nil the operation of natural selection.

Again, it should not be overlooked in this connection that in many of the annelids, as well as others, the most pronounced source of color is to be found in the hæmoglobin dissolved in the blood, and that it would be as futile to ascribe its color to natural selection as it would to claim a similar explanation of the color of the same substance in the blood of vertebrates, where, *as color,* it is absolutely of no selective value, except in such special cases as the colors of the cock's comb, where it may

come to play a secondary function as a sex character.

What shall be said of such forms as *Bipalium* and *Geoplana* among land planarians, which exhibit in many cases brilliant coloration, but since they are chiefly nocturnal in their habit and conceal themselves during the day under logs or other cover, the color could hardly serve any selective or adaptive function?

The same is equally true of such forms as nemerteans whose habitat is beneath the sand along the tide line or below, and also of many annelids having a similar habitat. Some of these, particularly among the latter, have types of coloration which are often of brilliant character and splendid patterns, vying, as one writer has expressed it, 'with the very butterflies.'

It can not be questioned that in some cases we find among these forms what would seem at first sight to be splendid illustrations of protective coloration. If, however, we trace in detail their distribution and variable habitat we shall often find, as did Semper in the case of *Myxicola,* that the supposed case of marvelous mimicry resolves itself into merest coincidence. This case cited by Semper is described in detail in 'Animal Life,' and its careful study by some of our over-optimistic selectionists would prove a healthy exercise, conducing to a more critical scientific spirit and, as a consequence, to saner interpretations of appearances in the light of *all* the facts.

The mimicry in the case was of coral polyps among which the annelid was found growing and which, in the form of its branches, their size and coloration, seemed so perfect that it had long escaped notice and was described by Semper as a new species.

It was found in various localities among the corals, but invariably having precisely the same simulation of the polyps, so that Semper noted it as among the finest cases of mimicry which had come to his attention. It so happened, however, that soon after he happened to discover his mimetic *Myxicola* growing upon a sponge whose color and form were so different as to render it very conspicuous. A systematic search for it in other situations soon revealed it among the rocks, and in his own language, 'Almost everywhere, and wherever I examined it carefully, it was exactly of the size and color of the polyps of *Cladocora cæspitosa.'*

Attention has already been called to Eisig's account of coloration among the Capitellidæ, in which he discards the factor of natural selection as wholly inadequate in the case of the organisms under consideration as well as in many others, and refers to many investigators who have likewise found it deficient. In his exhaustive monograph the subject is discussed in considerable detail and references given, which it would be impracticable to cite in such a review as the present.

It will be possible to refer but briefly to another group or two in the present discussion, the first of which is the echinoderms, and chiefly the starfishes. As is well known, these organisms exhibit a considerable range of variety and richness of coloration, among which red, orange, brown, yellow and black are more or less common. In not a few cases of course the colors comprise combinations of two or more of those named. An examination has been made of these pigments in a few cases and has sufficed to show that for the most part they are lipochromes and, therefore, belong to either reserve or waste products. Similar colors are also found among the brittle-stars, with occasional admixtures of blue or green, colors less common in the former group.

As is also well known similar colors are found among the crustacea, into a consid-

eration of which it is impossible to enter here. There is a matter, however, which I can not ignore in connection with the group, namely, the rather remarkable fact that in two phyla having so little in common as to habit, structure or environment, there should be so striking a color resemblance. This is further heightened by the fact that while one is a prey to almost every denizen of the sea of predatory habit, the other is almost correspondingly exempt. So far as I know echinoderms have few enemies, and are of course largely invulnerable against such as might otherwise find palatable feeding among these sluggish herds. If the color is in the one case protective, why not in the other? Or if it be not protective on the other hand, why claim such in the first? That sexual selection might have some place among crustacea may not seem improbable. But if color is its signal here what does it imply among echinoderms, where in the nature of the case it must be ruled out of account?

Discussing the significance of colors among the echinoderms Mosely submits the following interesting problem: "Those coloring matters which, like those at present under consideration, absorb certain isolated areas of the visible spectrum, must be considered as more complex, *as pigments,* than those which merely absorb more or less of the ends of the spectrum. * * * It seems improbable that the eyes of other animals are more perfect as spectroscopes than our own, and hence we are at a loss for an explanation on grounds of direct benefit to the species of the existence of the peculiar complex pigments in it. That the majority of species of *Antedon* should have vivid coloring matters of a simple character, and that few or only one should be dyed by a very complex one, is a remarkable fact, and it seems only possible to say in regard to such facts that the formation of the particular pigment in the animal is accidental, *i. e.*, no more to be explained than such facts as that sulphate of copper is blue."

Considered from the standpoint of metabolism such facts would hardly seem to assume the difficulty which might be implied in the case just cited, indeed they are in perfect alignment with what might be anticipated, and what has in cases previously cited been found to be actually occurring.

Similar conditions as to color and color significance are also matters of common knowledge in relation to mollusca. Perhaps few groups among animals exhibit more brilliant and varied colors than are to be found among gasteropods, yet in many of them this factor can have no more value as a means of adaptation than do biliary pigments or hæmoglobin among vertebrates, where as pigments their significance is nil. Of them, Darwin, with his usual frankness, has said, as previously cited, 'These colors do not appear to be of any use as a protection; they are probably the direct result, as in the lowest classes, of the nature of the tissues—the patterns and the sculpture of the shell depending on its manner of growth.' Referring in the same connection to the bright and varied colors of nudibranchs, he further declares, "many brightly colored, white, or otherwise conspicuous species, do not seek concealment; whilst again some equally conspicuous species, as well as other dull colored kinds, live under stones and in dark recesses. So that with these nudibranch molluscs, color apparently does not stand in any close relation to the nature of the place which they inhabit."

Into the classic shades afforded by the insects as a fruitful haunt and stronghold of natural selection I must not venture. Not that its problems have all been solved,

nor that some considered as settled beyond controversy may not have to be readjusted, not excepting the much exploited *Kalima* itself, but out of pure regard for the exigencies of the occasion.

No more dare I presume to enter the abysses of the deep sea and to pass in review its manifold and almost untouched problems of color significance, great as is the temptation and attractive as are its inducements. It must suffice to suggest that had half the ingenuity which has been exercised to bring these problems into alignment with the general sway and supposed supremacy of natural selection been employed in an analysis of the pigments and some efforts to discover the origin of coloration and its general significance as a physiological, rather than as a physical one, we should have been saved the sad rites attending the obsequies of still-born hypotheses and half-developed theories. The desperate attempt to save natural selection from drowning in its submarine adventures by lighting its abyssal path with the flickering and fitful shimmer of phosphorescence was worthy of a better cause. It is difficult to be serious with this phase of a subject the nature of which demands anything but ridicule or satire. But the attempts to illuminate the quiescent abysses with the dull glow which under all known conditions requires, if not violent, at least vigorous stimulus to excite it, and the assumption that its sources were sufficient to meet even a moiety of the necessities involved, makes a draft upon one's credulity which might arouse either indignation or the sense of the ludicrous, depending upon the point of view! But seriously, such a conception apparently loses sight of too many evident known conditions of phosphorescence with which we are familiar, not to mention the growing belief that the phenomenon is in itself of the nature of one of the wastes of metabolism to justify the herculean attempt to make it serve a cause so desperate.

As a concluding word allow me to say that in the present review I have not in the least sought to ignore or discredit the value of natural selection as a factor in organic evolution. Nor would I be understood as wholly discarding color as a factor in organic adaptation, particularly among the higher and more specialized forms, but rather to show its limits. At the same time I must submit to a growing conviction that its importance has been largely overestimated, and that other factors have been as largely lost sight of. If the present discussion may serve in even the smallest degree to direct attention to some of the latter it will have served its chief purpose.

CHARLES W. HARGITT.
SYRACUSE UNIVERSITY.

SCIENTIFIC BOOKS.

THE HONEYSUCKLES.*

THIS notable addition to the literature of the genus *Lonicera* is a most welcome contribution, presenting as it does the first complete systematic treatment of the honeysuckles since their description by De Candolle in the fourth volume of his 'Prodromus,' published in 1830. Mr. Rehder has consulted the specimens preserved in all the larger American herbaria, and in the most important of those of Europe, and has consulted the living collections in the larger botanical gardens, his investigations having extended through several years. The treatment of the genus in De Candolle's 'Prodromus' recognized 53 species, of which 42 are now held to be valid; the present monograph recognizes 154 species, together with 3 imperfectly known and not named, making 157 in all, thus adding 115 species to those known in 1830. In addition to these 157 species, a large number of varieties are given rank, as also are a considerable number of forms recognized under name;

* 'Synopsis of the Genus *Lonicera*,' by Alfred Rehder (*Ann. Rep. Mo. Bot. Gard.*, **14**: 27–232, *pl. 1–20*, October 8, 1903).